

Thesis/
Reports

PERKINS,
D.L.

LONG-TERM DYNAMICS OF WHITEBARK
PINE IN SAWTOOTH SALMON RIVER
REGION

Dendroecological Assessment
of
Whitebark Pine
in the
Sawtooth Salmon River Region Idaho

Dana L. Perkins
Laboratory of Tree-Ring Research
University of Arizona
Tucson, AZ 85721
phone: (520) 621-6469
USA

Forestry Sciences Laboratory
USDA-Forest Service
860 North 1200 East
Logan, UT 83407
USA
Phone: (520) 755-3560
email: dperkins@convx1.ccit.arizona.edu

and

Thomas W. Swetnam
Laboratory of Tree-Ring Research
University of Arizona
Tucson, Arizona 85721
USA
Phone: (520) 621-2112
email: tswetnam@ccit.arizona.edu

September 18, 1995

Abstract

Whitebark pine (Pinus albicaulis Engelm.) tree-ring chronologies of 700 to greater than 1,000 years in length were developed for four sites in the Sawtooth-Salmon River region, central Idaho. These ring-width chronologies were used to 1) assess the dendrochronological characteristics of this species, 2) detect annual mortality dates of whitebark pine attributed to a widespread mountain pine beetle (Dendroctonus ponderosae Hopk.) epidemic during the 1909 to 1940 period, and 3) establish the response of whitebark pine tree ring-width growth to climate variables.

Crossdating of whitebark pine tree-ring patterns were verified. Ring-width indices had low mean sensitivity (0.123–0.174) typical of high elevation conifers in western North America, and variable first order autocorrelation (0.206–0.551). Mountain pine beetle caused mortality of dominant whitebark pine peaked at 1930 on all four sites. Response functions and correlation analyses with state divisional weather records indicate that above average radial growth is positively correlated with winter and spring precipitation and inversely correlated with April temperature. These correlations appear to be a response to seasonal snowpack. Whitebark pine is a promising species for dendroclimatic studies.

Introduction

This research was initiated to study the dendroecology of whitebark pine (Pinus albicaulis Engelm.). Our objectives were to assess the dendrochronological characteristics of this long-lived pine, to evaluate the timing of a mountain pine beetle (Dendroctonus ponderosae Hopk.) epidemic that occurred in the early part of this century and to investigate the potential of whitebark pine for dendroclimatic research.

Concern over whitebark pine decline caused by exotic white pine blister rust (Cronartium ribicola J.C. Fisch.), infestations of mountain pine beetle, fire suppression and subsequent succession by shade-tolerant conifers (Arno and Hoff 1989, Keane et al 1989, Morgan and Bunting 1989, Keane and Arno 1993) has stimulated research on whitebark pine populations. Widespread mortality of whitebark pine and potential replacement by other tree species suggest changes in distribution and abundance of whitebark pine in the northern Rockies. Research on this species has concentrated in the intermountain region of western Montana and in the Greater Yellowstone ecosystem. (Arno 1986, Arno and Hoff 1989, Keane et al 1989) where environmental conditions favorable to the propagation of blister rust has resulted in severe pine mortality and reduced whitebark pine cone crops (Keane and Arno 1993, Kendall and Arno 1990, Mattson and Jonkel 1990).

The Sawtooth-Salmon River region, near the southern edge of whitebark pine distribution (Arno and Hoff 1989), appears to be a stronghold against the spread of white pine blister rust; but stands have sustained widespread mortality from bark beetle infestations. This area represents

a large geographic gap in whitebark pine research and in current tree-ring chronology networks. Schulman (1956) sampled 1,600 year old limber pines (Pinus flexilis James) near Ketchum Idaho, but no other sites with 1,000-year tree-ring chronologies have been developed for the northern Rockies. Consequently, we began this research to evaluate whitebark pine tree-ring chronologies as a source of long-term information on the historic ecological and climatic processes affecting subalpine ecosystems.

Whitebark pine is a slow growing, long-lived, stone pine (family Cembrae) of high elevation forests and timberlines of the northwestern United States and southwestern Canada. It occupies harsh, cold sites characterized by rocky, poorly developed soils and snowy, windswept exposures. Throughout its range whitebark pine may occur as an alpine species including a krummholz form in communities above tree line, as a seral species, or co-dominant with subalpine fir (Abies lasiocarpa (Hook) Nutt.) (Arno and Hoff 1989). Other common associates are lodgepole pine (Pinus contorta Dougl.), Engelmann spruce (Picea engelmannii Parry ex Engelm.), and mountain hemlock (Tsuga mertensiana (Bong) Carr.) (Arno and Hoff 1989).

Whitebark pine is a monoeious conifer with indehiscent cones that bear large wingless seeds. Clark's nutcracker (Nucifraga columbiana Wilson) is the primary dispersal agent of whitebark pine seeds and therefore are a critical component in their regeneration dynamics (Hutchins and Lanner 1982; Lanner 1982; Tomback 1982). Whitebark pine seeds are also important foods for red squirrels (Tamiasciurus hudsonicus), black bear (Ursus americana),

and endangered grizzly bear (Ursus horribilis). Natural mortality of whitebark is attributed to mountain pine beetle outbreaks and fire. These subalpine forests are valued as important wildlife habitats, watershed catchments, recreation areas and sensitive environmental indicators (Arno and Hoff 1989)

High elevation whitebark pine forests in central Idaho are composed of large diameter, old whitebark pine snags mixed with stands of live whitebark pine and subalpine fir. Mass mortality of mature age class trees has been attributed to a mountain pine beetle outbreak transmitted from lower elevation lodgepole forests to high elevation stands of whitebark pine (Arno and Hoff 1989, Bartos and Gibson 1990). This outbreak reached epidemic proportions from 1920 to 1940, and was reported from southern Canada to Wyoming (Arno and Hoff 1989; Ciesla and Furniss 1975). However, timing and patterns of mortality within and between whitebark pine stands are largely unknown. Specific questions arise from this lack of knowledge: Did the numerous dead overstory trees within stands succumb in a short period of a few years, or did they die over longer periods? Are mortality events synchronous among stands in the region? What were the climate conditions before, during and after the mortality? What are the interactions between climate variables and beetles? Is the mortality event unprecedented? While this study does not fully address or answer all these questions, it demonstrates the potential utility and value of tree-ring data for doing so.

Whitebark pine is a relatively new species of interest to dendrochronologists. Its ring-width series are known to crossdate and chronologies have

been produced from the Canadian Rockies, and eastern Oregon (Luckman 1993, 1994, Peterson 1990, and Parker unpublished data). However, dendrochronological characteristics and response to temperature and precipitation variables have not been described. The semiarid conditions of homogeneous, open canopied, high elevation stands in central Idaho favor the dendroecological study of whitebark pine in a setting nearly free from exotic blister rust fungus. This area is influenced by north Pacific weather patterns and is located in a transition zone between continental and inland-maritime climates (Arno and Hammerly 1984). Variability of continental atmospheric patterns in the transition zone, affects ecophysiological requirements of whitebark pine and mountain pine beetle. The dynamical feedbacks among these variables; trees, beetles and climate, is important for understanding changing environments. The vast pristine high elevation forests are relatively free of human disturbances such as logging and fuelwood collection. However, these areas have been affected by mountain pine beetle attacks, fires on some sites, fire suppression at most sites, and increasingly by recreational impacts. The opportunity to assess natural disturbance patterns and climatic factors affecting whitebark pine is essential to provide baseline reference for current and future changes in these valued subalpine habitats.

Methods

Site Descriptions

Four whitebark pine study sites were selected in central Idaho within the geographic region north of the headwaters of the Salmon River, south of the

Middle Fork of the Salmon River, west of the East Fork of the Salmon River and east of the North Fork of the Boise River (Figure 1). Two sites, Sandpass (SDP) and Upper Sandpass (UPS) are within the Sawtooth Wilderness area on the windward side of the northwest trending Sawtooth Mountains. The Railroad Ridge site (RRR), is in the lee of the northwest trending White Cloud Mountains, and the Twin Peaks site (TWP) is in the southeastern region of the Frank Church River of No Return Wilderness near Challis Idaho.

Whitebark pine stands in this region are typical of light-demanding conifers near timberline. They show increasing stand open-ness with elevation, often lack sharp stand boundaries and occur in an uneven mosaic pattern (Walter 1968, Tranquillini 1979). Tree distribution is limited by edaphic factors and wind rather than elevational constraints and associated temperature limitations. Ground cover is virtually non-existent on Sandpass, Upper Sandpass and Twin Peaks. The broad flat ridgetop of the Railroad Ridge site has ground cover composed primarily of Artemesia tridentata and Carex spp.

We selected classic dendroclimatic sites (Douglass 1941; Schulman 1956; Fritts 1976) characterized by steep exposed slopes, open grown stands, coarse well drained soils and southerly aspects to determine if whitebark pine in this region had sufficient climatic sensitivity to crossdate. These physical characteristics maximize climatic responsiveness of tree-ring width chronologies, while minimizing the influence of within-stand dynamics, such as competition and interference. Crossdating is the fundamental principle of dendrochronology. It is the property that cores sampled from different trees within a stand,

and cores from the same tree, share a common pattern of wide and narrow annual rings. The synchronicity of these patterns allows assignment of an exact calendar year to each tree-ring. (Douglass 1941, Fritts 1976).

Site elevations range from 2,800 to 3,000 meters. Site areas range from 1.5 to 4.0 hectares. The SDP and UPS sites occur on the divide between the Payette and Salmon River basins on the granitic contact between the Sawtooth and Idaho batholiths. These two sites are subject to the prevailing westerly weather patterns. The Twin Peaks site is rhyolitic substrate and the Railroad Ridge site is granitic. Physical site characteristics are summarized in Table 1.

This region is semiarid with 30 – 50 cm of precipitation a year, most of which falls as snow and rain during the winter and spring. At elevations above 2,700 meters, most precipitation falls as snow. Annual temperatures range from average minimums of -7°C to average maximums of 11°C . Extreme cold temperatures from -34 to -47°C are recorded from December through February. Winds redistribute snow around whitebark pine trees to form snowdrifts that may linger until July and occasionally August. In open areas, but not too distant from clumps of trees and associated snowdrifts, remnant dead and subfossil wood is abundant. The semiarid nature of this region preclude rapid decay of these fallen trees.

Field Collections

Tree-Ring Width Chronologies

Field collections were made to develop master ring-width chronologies on each of the four sites using standard dendrochronological procedures (Fritts 1976, Swetnam et al 1985). Fifteen to thirty live and/or dead trees were sampled on each site during the growing season 1992-1993. Intermediate, codominant and dominant size classes were sampled with emphasis on old trees with flat tops, heavy drooping limbs, exposed roots, and limb and leader dieback. Photographs were taken of all trees sampled. At least two cores were extracted from each tree using a 20" increment borer. Diameter breast height (DBH) and estimated heights were recorded.

Mortality and Size-Class Sampling

A sampling strategy based on distance methods (Pollard 1971, Smeins and Slack 1978) was used to determine the relative frequency of trees killed by mountain pine beetle and to characterize stand structure. Relative frequency, F_i , is expressed as $\%F_i = n_i/n(100)$ where n_i is phenomena of interest (size or mortality class), and n is the the total number of occurrences of the phenomena of interest (total trees sampled). Transects were systematically established on 200 ft topographic contours (level curves) across each site. On each transect, plot centers were located at random distances. From each plot center we recorded the distance (meters) to the nearest two trees. We used both trees at each sample plot to record mortality and size-class frequencies.

A consequence of seed dispersal by Clark's Nutcracker is that whitebark pine have a spatially clumped distribution (Lanner 1980, Sudworth 1980, Tomback 1982). Clumps are composed of genetically distinct stems (several trees) or genetically identical, multistemmed individuals (one tree). To meet random distribution assumptions, we consider the clumps, rather than tree stems, to be randomly distributed.

Mortality patterns were described by recording whether the tree was live (L), dead by an unknown cause (U), or dead due to beetle kill (B). The latter was determined if adult mountain pine beetle galleries, which appear as distinctive vertically aligned 'J' shaped marks (Wood 1982), were observed on the bole. Dead trees and subfossil wood without beetle galleries were coded unknown dead. At least two increment cores were extracted from all beetle-killed trees.

To describe stand structure patterns, we recorded diameter breast height (DBH), estimated height and coded cohorts according to the following criteria: seedling (s), those trees less than 1 inch (2.54 cm) in DBH and under a foot (30.5 cm) tall, sapling (S), less than 1 inch (2.54 cm) to 4 inches (10.2 cm) DBH and greater than a foot (30.5 cm) tall, intermediate (i), 4 to 8 inches (10.2 – 25.8 cm) DBH, co-dominate (c), 8 to 19 inches (25.8 – 48.3 cm) DBH and dominant (d), greater than 19 inches (48.3 cm) DBH.

Laboratory Analysis

Tree-Ring Chronology Development and Assessment

Increment cores were mounted in wooden holders and surfaced with sandpaper to reveal ring boundaries and diagnostic ring structures. Measurements of ring widths were made with a sliding-stage micrometer interfaced with a microcomputer (Robinson and Evans 1980).

Crossdating consisted of combined traditional techniques of skeleton plotting (Stokes and Smiley 1968; Swetnam et al 1985), and the use of quality control crossdating program, COFECHA, to ensure measured series were accurately dated (Holmes 1983). The COFECHA algorithm calculates running correlation coefficients between a single series and the master composite that excludes the series being tested. Crossdating was confirmed if the highest significant correlation occurred at the dated position. If COFECHA suggested an alternative position, the core was visually examined to confirm the suggested re-positioning. After crossdating was assured by the above methods, each series was standardized to remove biological age and stand-related (endogenous) trends (Fritts 1976, Cook and Holmes 1984).

The mathematical standardization function that has the most widespread application for semiarid open-grown conifers is the negative exponential curve, $y = ae^{-bt} + k$ (Fritts 1969). The coefficients, a , b and k are estimated for each series and the series is normalized (divided) by this curve.

The theoretical justification for this detrending method is that a negative exponential function idealizes the addition of wood volume to a cylinder, which biologically reflects the geometric growth of a tree bole (Fritts 1969).

All series with this type of monotonically decreasing growth trend were standardized in this manner. If the coefficients b , a are negative then a straight line of appropriate slope was fitted to the series. Division of the observed ring-width values by the expected values calculated from the selected detrending function produce the index value for the series.

For series with oscillatory growth trends, we chose a 100-year smoothing spline (Cook and Peters 1981; Reinsch 1967) that preserves 50% of the variance at the 100-year wavelength. Generally this detrending method removes the inter-decadal to sub-century length trends in the ring-width series caused by non-climatic endogenous stand dynamics (Cook and Peters 1981, Cook 1985). For instance, growth releases following the creation of canopy gaps, after insect attack or fire, are usually removed by this type of detrending.

After division of each series by a negative exponential function, linear function or 100-year smoothing spline, the series were averaged to produce a master index chronology for the site. Selection of the detrending options and development of the final master chronologies was performed with procedures in computer program ARSTAN (Cook 1985). Sandpass and Upper Sandpass were standardized with a combination of the negative exponential, linear or 100-year smoothing spline and all series at the Twin Peaks and Railroad Ridge sites were standardized with the the 100-year smoothing spline.

Correlation analyses, and standard descriptive statistics were used to compare dendrochronological characteristics between whitebark pine master chronologies for the four sites. The new chronologies were also compared to other chronologies on sites with same or similar species type, sim-

ilar site elevation, and geographic proximity. These include a Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) chronology from near Ketchum, Idaho, a Douglas-fir chronology near Salmon Idaho, three whitebark pine chronologies from near Joseph, Oregon and one rocky mountain juniper (Juniperus scopulorum). chronology near Jarbridge Nevada.

A Fast Fourier Transform (FFT) algorithm (Press et al 1988), which preserves the spectral trends of time series, was derived for each chronology and overlain on the master chronology for visual comparison of trends. The interval chosen for this analysis was 8 years.

Mortality Assessment

Increment core samples from the mountain pine beetle-killed trees were skeleton plotted and visually crossdated with the master chronologies. Two criteria were considered to record the year of mortality of a whitebark pine: (1) observed adult beetle galleries on the bole and (2) dating of outer ring of against crossdated series and chronology. Measured ring-widths were processed through program COFECHA, to verify crossdating and the outside ring date.

Dendroclimatic Assessment

Simple correlations and response functions (Fritts 1971, 1976) were calculated to assess whitebark pine annual ring growth response to monthly average temperature and total precipitation factors. Response function analysis regresses principal components (eigenvectors) of climate variables upon the

master index chronology to calculate a set of coefficients (weights) that correspond to the original set of climate variables. A computer routine samples many times with replacement to generate empirical estimates of the entire sampling distribution, from which confidence intervals are computed for the response coefficients (Fritts 1993). Meteorologic data for the central mountain region of Idaho, compiled by the National Climatic Data Center, NOAA, Asheville, North Carolina for the 95 year time period, 1896-1991 were used for this analysis. This is a composite data set, based on homogeneity of weather patterns within a geographic region. Divisional data set, Idaho 1003, was selected because nearby weather stations were scarce, were situated at low elevations, and data sets had many missing values. Monthly total precipitation and monthly average temperature values for a fourteen month period starting in July through the following August were selected as the climatic variables. Three years prior growth was also used to assess autocorrelation affects.

Results and Discussion

Tree-Ring Width Chronologies

Whitebark pine tree-ring chronologies from central Idaho constitute the first millennium-length chronologies constructed from the northern Rocky Mountain region in the United States. The discovery of the oldest living whitebark pine known in North America was made in the Sawtooth-Salmon River region during this study. This tree exceeds 1,270 years in age. The innermost

ring of an increment core that did not include the pith was 726 A.D. Whitebark pine is now eleventh on the longest-lived tree species list, subsequent to Douglas-fir (Brown 1994). The largest whitebark pine on the National Register of Big Trees, also occurs in this region; it exceeds 8.5 feet (260 cm) diameter breast height.

Crossdating Characteristics

Crossdating of these trees was successful, but not easy. Narrow-ring signature years common to most sites aided crossdating efforts, but lack of high frequency variation of ring-widths made the task difficult with some cores. Old, large-diameter trees crossdated well with each other and comprise the master chronology. On all sites, the crossdating of the intermediate and codominant trees with the dominant and old trees was poor. The strength of crossdating among these trees was highest for Sandpass and Twin Peaks as reflected by an interseries correlation above 0.6 (Table 2). Upper Sandpass and Railroad Ridge had interseries correlations above 0.5. Trees with interseries correlations near and below 0.43 were regarded as unacceptable and were not included in the master ring-width chronologies.

The complacent nature of many segments of the ring-width series, the occurrence of heart rot, and the low sample depth before 1300 A.D., prevented us from including some live, some standing dead and several remnant down and dead samples to the master ring-width chronologies. Sample depth, the number of trees that are included in the chronology in a given calendar year, dropped off rapidly before 1300 A.D. and after 1930 (Figure 2). Increased

sampling efforts, particularly of dead and remnant wood, may allow future development of chronologies with robust sample depth in the 700 to 1300 year period.

Master Chronologies

Master chronologies scaled to the time period, 760 A.D. to 1991, overlain with the FFT smoothed curve, revealed low frequency variation from 1300 A.D. to the present (Figure 2). The large amplitude of ring width variations between 970–1300 was likely a consequence of few samples and juvenile growth patterns. (Figure 2). Generally, as young trees mature, annual ring increment increases to a maxima, then decreases exponentially to an asymptotic ring-width level.

Mean sensitivity, defined as the average absolute difference between two adjacent ring-width measurements divided by their mean measurement (Douglass 1936), ranges between 0.12 on the UPS site to 0.17 on TWP, RRR and SDP sites and is representative of the low year to year variance typical of Rocky Mountain conifers at high elevation sites (LaMarche and Stockton 1974, Fritts and Shatz 1975). First order autocorrelation coefficients range from 0.21 at the Twin Peaks site to 0.55 at the Sand Pass site. This is a measure of the average dependence of a ring width value at year t relative to the ring width value at year $t - 1$. High autocorrelation coefficients are typical of high elevation tree-ring chronologies (LaMarche and Stockton 1974, Fritts and Shatz 1975). We note that the Sandpass and Railroad Ridge sites

are typical in this response whereas Upper Sandpass and Twin Peaks are less autocorrelated (Table 2).

Visual comparisons of master skeleton plots and correlation analysis with Idaho, Douglas-fir, Oregon, whitebark pine and Nevada, Rocky Mountain juniper chronologies, revealed no crossdataability with the exception of one whitebark pine chronology, from near Joseph, Oregon (CHJOE2). Possible explanations for non-crossdataability, include site differences (e.g. elevation, substrate, aspect), distance from region of study, differential species response to climate variables and climatic pattern variation. Strong positive correlations among the four Sawtooth Salmon River region whitebark pine chronologies for the 1300-1991 period, and positive association with the eastern Oregon chronology (Parker unpublished data, 1860-1964 period) are shown in a correlation matrix (Table 3). SDP and TWP exhibit the strongest correlation. RRR is the least well correlated with the other sites.

Mountain Pine Beetle Caused Mortality

Calendar dates were determined for the mountain pine beetle outbreak of the early twentieth century. The distribution of crossdated beetle kill trees starts in the early 1920s and clusters around a single peak maximum at 1930 on all four sites (Figure 3). These observations are in agreement with the documented mountain pine beetle infestation in lodgepole pine in central Idaho. In a 1929 letter to the District Forester in Ogden Utah, the Challis Forest Supervisor reports that infestation reached epidemic stage in lodgepole pine, in the summer of 1926. He noted that although the chief host was lodgepole

pine, whitebark pine and limber pine were also infected and appeared less resistant to beetle attack than lodgepole (Renner 1929). One tree on the UPS site died in 1819 and had observable mountain pine beetle galleries on the stem. This is the only tree in our sample base that we suggest was killed by mountain pine beetle before the 20th century epidemic.

Laboratory analysis of all trees with adult mountain pine beetle galleries, revealed the presence of blue stain fungi (Ophiostoma clavigerum) in the outer sapwood. This fungi is associated with several species of bark beetles, (Harrington 1987) and is not a sufficient criteria alone to indicate mountain pine beetle presence. Blue stain fungi, however, may be viewed as a secondary indicator of bark beetle presence. In addition to the beetle-killed tree mortality dates shown in Fig. 3, two dead trees with blue stain fungi looked like probable beetle kill trees in the field. Death dates were 1730 and 1887. The weathering of the bole prevented us from confirming the presence of adult galleries on these trees.

The magnitude of the 1930 outbreak is apparent from the relative frequency of mountain pine beetle killed whitebark pine. On three sites, 22% of the total trees sampled were mountain pine beetle-killed. On four sites, live codominant and dominant trees comprised less than or equal to 9% of the total sample, and young size class trees, seedlings, saplings, and intermediates comprise 56-74%. (Table 4). From the dead tree subset of the total sample, the relative frequency of beetle killed trees was 20% on SDP, 61% on UPS, 69% on TWP and 58% on RRR. The ratio of beetle-killed snags to large diameter size class snags was 67, 57, 100, 52% for the respective sites.

Interpretation of the subset data is statistically tenuous because the ratio of random variables may result in a nondifferentiable distribution function. However, the relative frequency of size class data, dramatic decrease of dominant whitebark pine trees near 1930 (Figure 2) and synchronous crossdated beetle-kill dates over the Sawtooth-Salmon river region, exemplify the magnitude and scope of the mid 1920's-early 1930's mountain pine beetle epidemic.

SDP and TWP master chronologies from 1850 to the present show general synchronous patterns punctuated by narrow ring marker years, 1885, 1895, 1915, 1928, 1934, 1939, and 1969. The mountain pine beetle infestation occurred during the longest sustained low growth period for the last 200 years (Figure 4). The duration of the epidemic in whitebark pine was approximately 8 - 12 years and was typical of the range of infestation in the most common host, lodgepole pine. (Roe and Amman 1970, Cole and Amman 1980).

Climate-Tree-Growth Relationships

Whitebark pine is a promising species for dendroclimatic studies of the transitional climate zone of the northern Rockies. Sandpass and Twin Peaks tree-ring width chronologies showed the most pronounced response to climate variable analysis. Results for those sites are reported here (Figure 5). Response functions for the Sandpass standardized chronologies revealed 48.0% of the variance (r^2 adjusted) in ring width is explained by climate variables, while 8.0% was explained by prior growth. This was a total of

56.0% variance explained by the abiotic and biotic components of this system (Figure 5). For the Twin Peaks site, standardized chronology, 39.0% of the variance in ring width was explained by climate variables, and 12.0% was explained by prior growth, for a total variance of 51.0% (Figure 5). The third and second years previous growth was significant on the SDP and TWP sites respectively (Figure 5). This is a low contribution by previous growth relative to other tree-ring chronologies used in dendroclimatic work (Fritts 1992), particularly high elevation conifers (La Marche 1974, LaMarche and Stockton 1974). The low importance of autocorrelation in these results was confirmed by computing correlation and response functions using chronology residuals from autoregressive models (i.e. whitened series). Similar results to the standard chronologies were obtained.

Correlation and response function analyses revealed above average ring width growth was positively correlated with winter and spring precipitation, and inversely correlated with April and May temperature (Figure 5). Our interpretation is that above average growth occurs with abundant snow-pack and cool spring temperatures. The onset of June and July heat with continued cool nights, produce gradual snow melt and adequate soil water availability for whitebark root systems.

On high elevation sites in North America, correlations of tree growth with climate variables typically respond positively to winter and spring precipitation and summer temperature. (Kienast and Schweingruber 1986, Graumlich and Brubaker 1985, Peterson et al 1990, and others) Whitebark pine is similar

in this response, with June temperature, positively correlated and statistically significant ($p < 0.05$) on the SDP site, but not statistically significant on TWP. The feedbacks among spring precipitation and temperature variables likely produce nonlinear interactions affecting snowpack. Results from this work suggest that open grown stands of high elevation whitebark pine on classic dendroclimatic sites may serve as proxy records of regional weather patterns.

Conclusions

Attempts to understand processes governing forest ecosystems are plagued by short data sets and compounded by the long generation time of trees. Preliminary dendroecological analysis of high elevation homogenous whitebark pine stands on classic dendroclimatic sites generated time series greater than 700 years. We have shown that whitebark pine tree-ring chronologies, reveal patterns associated with the biotic and abiotic factors affecting the their growth. These long time series are essential for recording the cyclicity of disturbance events and are good candidates for dendroclimatic research. As such, whitebark pine tree rings may serve as a type of subalpine clock. The southern Idaho semiarid climate favors preservation of high elevation remnant wood. It is therefore possible to increase the sample size and replication in earlier time periods included in our current chronologies, so that ecological and climatic investigations could be extended back into the first millennium A.D. These chronologies have filled a small geographic gap in the North American tree-ring network, particularly of high elevation sites.

The ability to map a mountain pine beetle epidemic in the time domain was demonstrated. A logical continuation of this research would generate spatial maps of the mountain pine beetle outbreak using the methods established here. Decay and loss of sapwood may limit the accurate dating of time of death to subsets of trees and sites. The potential to expand this sampling to other locations could resolve spatial and temporal patterns of mountain pine beetle infestations on stand level to regional scales.

Acknowledgements

We thank Tom Harlan, Denis Norton, Tony Caprio, Bob Lofgren, Henri Grissino-Mayer, Chris Baisin, Ed Wright, and Hal Fritts for assistance, expertise and discussion throughout the project. We are grateful to Sandy Gebhards, Carolyn Perkins, Sandy Craig, and Andrea Hernandez for mountain field assistance. ~~Funding for this research was provide by the USDA Forest Service, Intermountain Region, agreement No. INT-92693.~~ Thanks to the group effort by projects 45102, others need to list ... and the Challis and Sawtooth National Forests. We heartily thank Dick Krebill, Doug Fox, and Wyman Schmidt, Ward McCaughey, Carl Pence, Dave Reeder, Jim Brown, Gene Amman, Steve Arno, and Penny Morgan.

References

- Arno, S.F. and Hammerly, R.P. 1984. Timberline: Mountain and Arctic Forest Frontiers. The Mountaineers, Seattle.
- Arno, S.F. and Hoff, R.J. 1989. Silvics of Whitebark pine (Pinus albicaulis). USDG For. Serv. Gen. Tech. Rep. INT-253.
- Amman, G.D. 1977. The role of mountain pine beetle in lodgepole pine ecosystems: impact on succession. In The role of arthropods in forest ecosystems: Proceedings, 15th international congress of entomology, 19-27 Aug, 1976, Washington, DC. Edited by W.J. Mattson. Springer-Verlag, New York. pp. 3-18.
- Amman, G.D. 1978. Biology, ecology, and causes of outbreaks of the mountain pine beetle in lodgepole pine forest. In Proceedings; Theory and practice of mountain pine beetle management in lodgepole pine forest. 25-27 April 1978, Pullman, W.A., Moscow, ID. Edited by A.A. Berryman, G.D. Amman, and R.W. Stark. University of Idaho, Forest, Wildlife and Range Experiment Station, Pullman, W.A., Moscow, I.D. pp. 39-53.
- Bartos, D.L. and Gibson, K.E. 1990. Insects of whitebark pine with emphasis on mountain pine beetle. In Proceedings-Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource. 29-31 Mar. 1989, Bozeman, M.T. Compiled by W.C. Schmidt

and K.J. MacDonald. USDA For. Serv. Res. Gen. Tech. Rep. INT-270. pp. 171-174.

Brown, P.M. 1994. Oldlist: A database of maximum tree ages. In Proceedings of the International Conference on Tree Rings, Environments and Humanity, 16-21 May 1994, Tucson, A.Z. Special issue Radiocarbon. In press.

Ciesla, W.M. and Furniss, M.M. 1975. Idaho's haunted forests. American Forests. 81(8): 32-35.

Cole, W.E. and Amman G.D. 1980. Mountain pine beetle dynamics in lodgepole pine forests part 1: Course of an Infestation. USDA For. Serv. Gen. Tech. Rep. INT-89.

Cook, E.R. 1985. A time series approach to tree-ring standardization. Ph.D. dissertation, University of Arizona, Tucson.

Douglass, A.E. 1936. Climatic cycles and tree growth, Vol. III. A study of cycles. Carnegie Inst. Wash. Publ. 289.

Douglass, A.E. 1941. Crossdating in dendrochronology. Journal of Forestry 39: 825-831.

Fritts, H.C. 1976. Tree Rings and Climate. Academic Press, New York.

Graumlich, L.J. and Brubaker, L.B. 1986. Reconstruction of annual temperature (1590-1979) for Longmire, Washington, derived from tree-rings. Quat. Res. 25: 223-234.

- Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measuring. *Tree Ring Bull.* **43**: 69-78.
- Holmes, R.L., Adams, R.K. and Fritts, H.C. 1986. Tree-ring chronologies of western north America: California, eastern Oregon and northern great basin. Quality control of crossdating and measuring: A users manual for program COFECHA. Chronology Series 6. Laboratory of Tree-Ring Research, University of Arizona.
- Hutchins, H.E. and Lanner, R.M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. *Oecologia.* **55**: 192-201.
- Keane, R.E., Arno, S.F., Brown, J.K., and Tomback, D.F. 1990. Modelling stand dynamics in whitebark pine (*Pinus albicaulis*) Forests. *Ecol. Model.* **51**: 73-95.
- Kendall, K.C. and Arno, S.F. 1990. Whitebark pine—an important but endangered wildlife resource. In Proceedings—Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource. 29–31 Mar. 1989, Bozeman, M.T. Compiled by W.C. Schmidt and K.J. MacDonald. USDA For. Serv. Res. Gen. Tech. Rep. INT-270. pp. 264–273.
- Kienast, F. and Schweingruber, F.H. 1986. Dendroecological studies in the Front Range, Colorado, U.S.A. *Arctic and Alp. Res.* **18** :277-288.

- LaMarche, V.C. Jr. 1974. Frequency-dependent relationships between tree-ring series along an ecological gradient and some dendroclimatic implications. *Tree-Ring Bull.* **34**: 1-20.
- LaMarche, V.C. Jr. and Stockton, C.W. 1974. Chronologies from temperature-sensitive bristlecone pines at upper treeline in western United States. *Tree-Ring Bull.* **34**: 21-45.
- Lanner, R.M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. *Can. J. For. Res.* **12**(2):391-402.
- Luckman, B.H. 1994. Using multiple high-resolution proxy climate records to reconstruct natural climate variability. In *Mountain Environments in Changing Climates*. Edited by M. Beniston. Routledge Press, London. pp. 42-59.
- Luckman, B.H. 1993. Evidence for Climatic conditions between ca. 900-1300 A.D. in the Southern Candian Rockies. *Climate Change*. **26**(2-3): 171-182.
- Mattson, D.J. and Jonkel, C. 1990. Stone pines and bears. In *Proceedings--Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource*. 29-31 Mar. 1989, Bozeman, M.T. Compiled by W.C. Schmidt and K.J. MacDonald. USDA For. Serv. Res. Gen. Tech. Rep. INT-270. pp. 223-236.

- Morgan, P. and Bunting, S.C. 1989. Fire effects in whitebark pine forests. In Proceedings-Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource. 29-31 Mar. 1989, Bozeman, M.T. Compiled by W.C. Schmidt and K.J. MacDonald. USDA For. Serv. Res. Gen. Tech. Rep. INT-270. pp. 166-170.
- Pollard, J.H. 1971. On distance estimators of density in randomly distributed forests. *Biometrics*. **27** : 991-1002.
- Peterson, D.L. 1990. Growth trends of whitebark pine and lodgepole pine in a subalpine Sierra Nevada forest, California, U.S.A. *Arctic and Alp. Res.* **22**: 233-243.
- Press, W.H., Flannery, B.P., Teukolsky, S.A., and Vetterling, W.T., 1988. *Numerical Recipes in C*. Cambridge University Press, London.
- Reinsch, C.H. 1967. Smoothing by spline functions. *Numerische Mathematik* **10**: 177-183.
- Roe, A.L. and Amman G.D. 1970. The mountain pine beetle in lodgepole pine forests. USDA For. Ser. Res. Rep. INT-71.
- Schulman, E. 1956. *Dendroclimatic Changes in Semiarid America*, University of Arizona Press, Tucson, Arizona.
- Smeins, F.E. and Slack, R.D. 1978. *Fundamentals of Ecology Laboratory Manual*. Kendall/Hunt Publishing Company, Dubuque, Iowa.

- Stokes, M.A. and Smiley, T.L. 1968. An Introduction to Tree-Ring Dating. University of Chicago Press, Chicago.
- Swetnam, T.W., Thompson, M.A. and Sutherland, E.K. 1985. Using dendrochronology to measure radial growth of defoliated trees. USDA For. Serv. Agric. Handb. 639.
- Tomback, D.F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: A mutualism hypothesis. J. Anim. Ecol. 51: 451-467.
- Tranquillini, W. 1979. Physiological Ecology of the Alpine Timberline. Springer-Verlag. Berlin.
- Walter, H. 1968. Die Vegetation der Erde in öko-physiologischer Betrachtung. Band II. Jena: VEB Gustav Fischer.
- Wood, S.L. 1982. The Bark and Ambrosia Beetles of North and Central America (Coleoptera: Scolytidae), a Taxonomic Monograph. Great Basin Naturalist Memoirs, No 6. Brigham Young University.

Figure 1: Map of the Sawtooth-Salmon River region, Idaho, showing white-bark pine study sites.

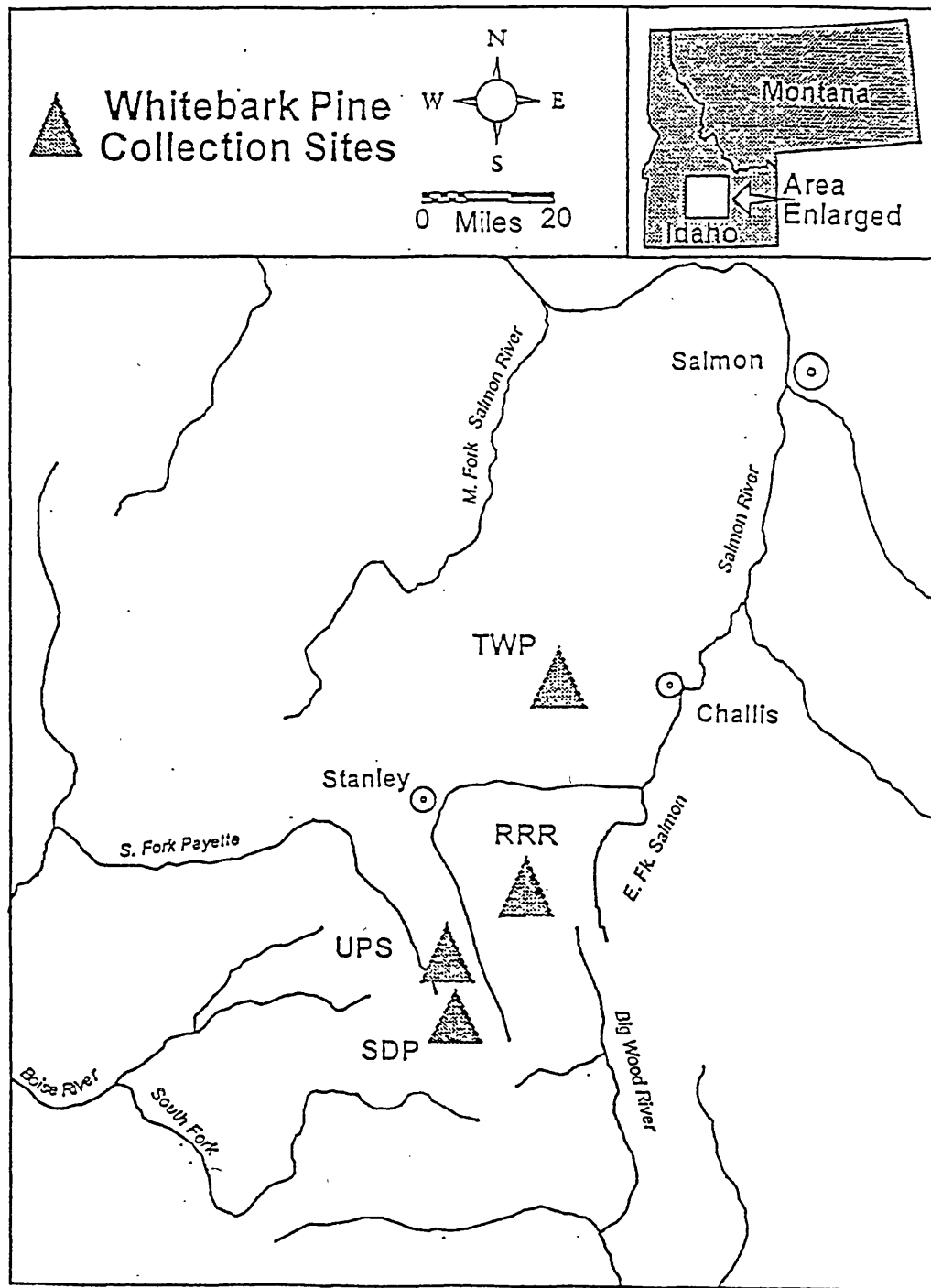


Table 1: Whitebark pine site descriptions.

	Sandpass	Upper Sandpass	Twin Peaks	Railroad Ridge
Latitude	43°58'15" N	43°58'28"N	44°36'03"N	44°08'25"N
Longitude	114°58'06" E	114°58'02" E	114°27'46" E	114°33'07" E
Elevation	2800 m	2800 m	2800 m	2930 m
Aspect	S-SE	WSW-W	S	S-SE
Slope	5 – 30°	20 – 35°	15 – 30°	5 – 30°
Soil	granite	granite	rhyolite	granite
Site Area	3.0 ha	2.2 ha	1.5 ha	4.0 ha

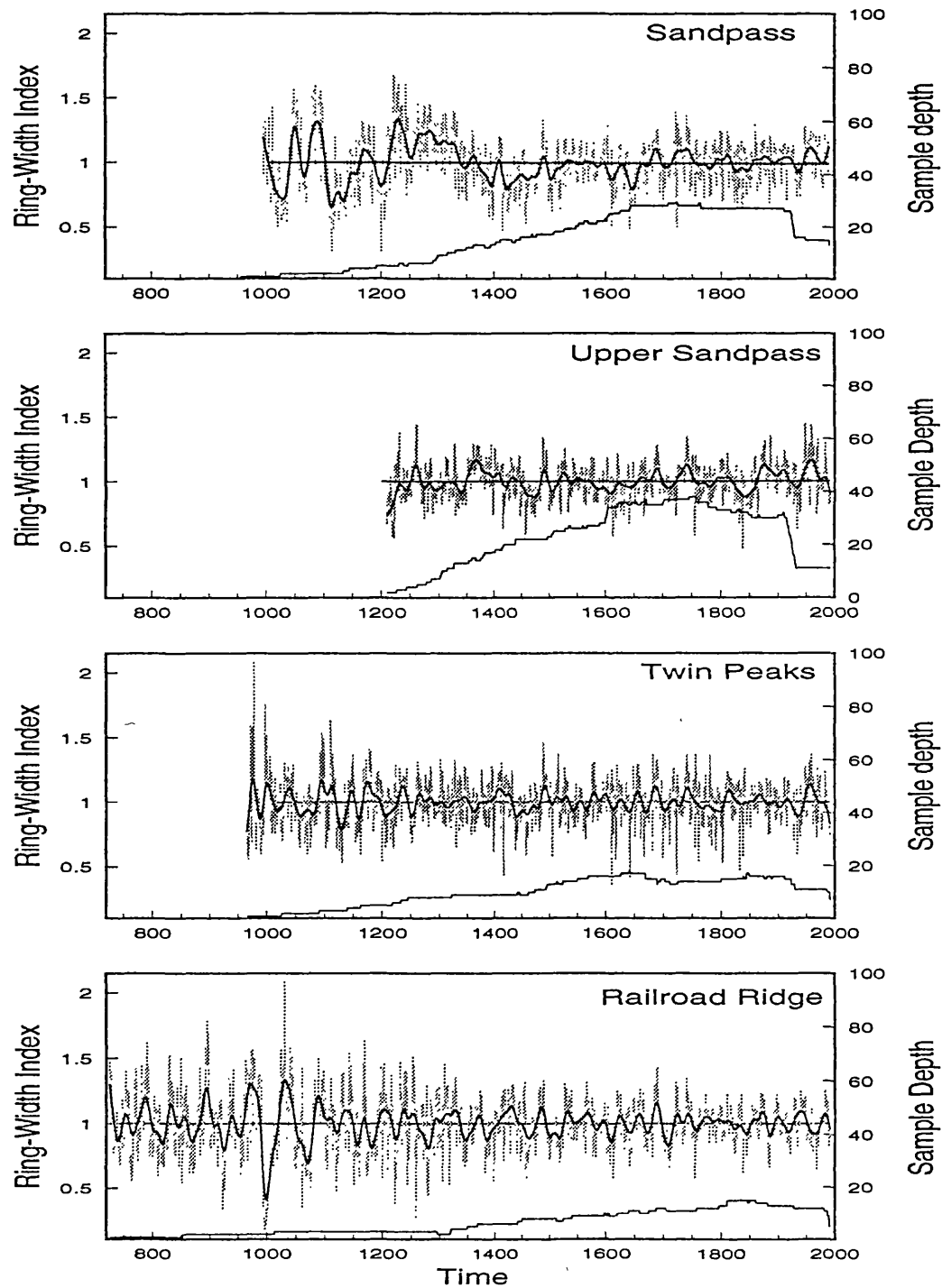


Figure 2: Whitebark pine master ring-width chronologies, scaled to a common interval and overlain with a Fast Fourier Transform smoothing function to accentuate inter-decadal trends. Sample depth, the number of trees represented in the chronology at a particular year, is plotted on the right hand axis.

Table 2: Whitebark pine chronology statistics.

	Sandpass	Upper Sandpass	Twin Peaks	Railroad Ridge
Length [yrs]	1037	783	1028	1267
Number of trees	19	28	12	11
Number of cores	37	52	29	22
Mean Ring-Width [mm]	0.46	0.33	0.39	0.49
Inter-Series Correl.	0.63	0.56	0.62	0.57
Mean Sensitivity	0.17	0.12	0.17	0.17
First Order Autocorrel.	0.55	0.29	0.21	0.48

Table 3: Correlation matrix for whitebark pine tree-ring chronologies, central Idaho and eastern Oregon. Time periods for comparison are 1300–1991, except for correlations with the eastern Oregon site, CHJOE2, which were 1860–1964.

	SDP	UPS	TWP	RRR	CHJOE2
SDP	1.0				
UPS	0.64	1.0			
TWP	0.65	0.59	1.0		
RRR	0.48	0.51	0.46	1.0	
CHJOE2	0.30	0.19	0.30	0.28	1.0

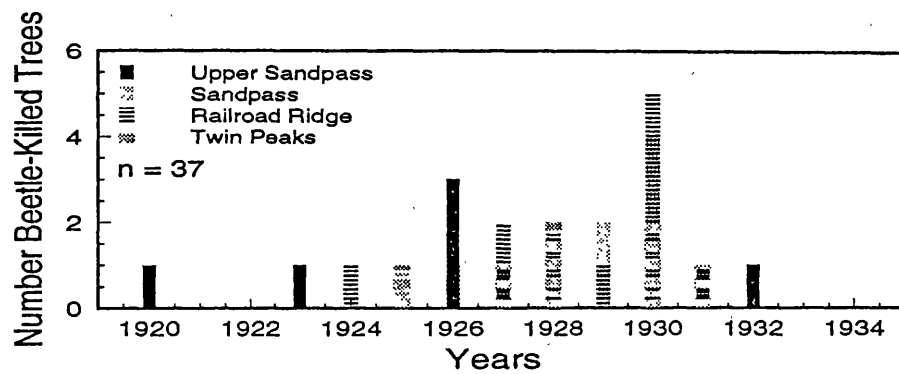


Figure 3: Crossdated death dates of thirty-nine whitebark pine killed by mountain pine beetle. Mortality reaches a maximum at 1930.

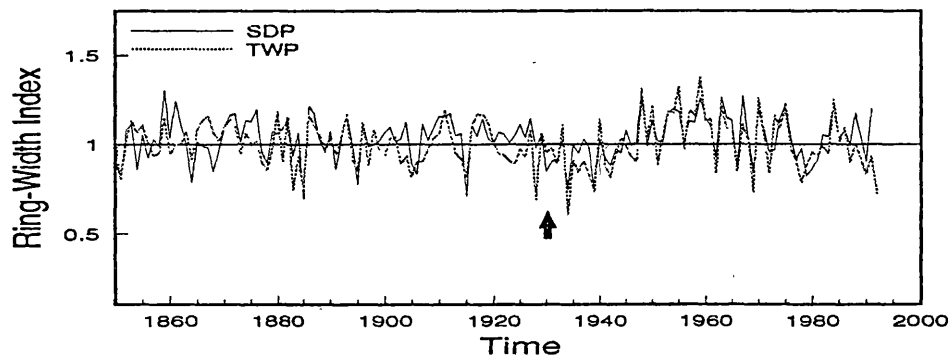


Figure 4: SDP and TWP master chronologies for 1850 to 1991. Arrow indicates peak of mountain pine beetle-kill in whitebark pine.

Table 4: Whitebark pine stand structure summary. Trees killed by mountain pine beetle had distinct J-shaped adult galleries on the stem. Trees were coded unknown dead when galleries weren't observable.

	SDP	UPS	TWP	RRR
Number of plots	47	25	18	35
Number of trees inventoried	94	50	36	71
Relative Frequency[%]				
Live trees	78	64	64	66
Dead trees	22	36	36	34
Subset of dead trees				
Beetle-killed trees	4	22	25	20
Unknown dead	18	14	11	14
Relative Frequency[%]				
Seedlings	29	8	22	10
Saplings	34	38	30	34
Intermediates	11	10	14	13
Codominants	3	2	0	8
Dominants	1	6	0	1

Figure 5: Correlations and response functions. Correlation coefficients are significant ($p < 0.05$) for $|r| = 0.210$ for Sandpass and Twin Peaks.

